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R. R. Hopcroft · J. C. Roff

Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods

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Abstract Egg production was measured in 17 species of copepods from the genera *Acartia*, *Calanopia*, *Centropages*, *Clausocalanus*, *Corycaeus*, *Eucheata*, *Euterpina*, *Oithona*, *Oncaea*, *Paracalanus*, *Parvocalanus*, *Temora* and *Undinula* in Jamaican waters. At the high local temperatures (~28 °C), mean egg production ranged from 3.2 to 88 eggs female^{-1} d^{-1}, and instantaneous female growth (g, as egg production) ranged from 0.04 to 0.87 d^{-1}. Female growth was positively related to ambient chlorophyll concentration ($r^2 = 0.44$) and negatively to female body size ($r^2 = 0.29$). Together these two variables explained 60% of the variation in growth. When quadratic terms for chlorophyll and a term for interaction of body size and chlorophyll were introduced, 82% of the variance in growth rate was explained. Egg production rates represent an extension of the resource and size-dependent relationship established for copepodites. In smaller species (< 3.5 μg), egg production was comparable to prior copepodite somatic growth; in larger species (> 3.5 μg), egg production is compromised at lower resource concentrations than copepodite somatic growth. Thus, it appears that egg production in tropical copepods may be frequently limited by resources in a size-dependent manner. Under conditions where growth is resource limited, we caution against the application of egg production rates for the calculation of total copepod production.

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R.R. Hopcroft (✉)[1] · J.C. Roff
Department of Zoology, University of Guelph,
Guelph, Ontario, N1G 2W1, Canada

Present address:
[1]Monterey Bay Aquarium Research Institute,
7700 Sandholt Rd., Moss Landing,
California 95039-0628, USA

Introduction

In our quest to understand the functioning of marine ecosystems, much research has focused on the copepods. In turn, most copepod research has focused on the adult, particularly the female, because it is the largest, longest lived, and most easily identifiable stage. Our appreciation of any organism's importance in an ecosystem is ultimately dependent on detailed knowledge of rates of processes (Longhurst 1984). Of all the rate processes involved in copepod life cycles, we know more about egg production than any other activity (with the possible exception of grazing).

The study of egg production has theoretical as well as logistical appeal. From a conceptual standpoint, the number of eggs produced per female is a fundamental property that should have bearing on the observed and potential numerical responses of populations to their environment. From a practical standpoint, the measurement of egg production requires few resources and – once an experimenter is proficient – relatively little investment in time. Results are clear, involving simple counts of eggs (and possibly nauplii) and – compared to most other estimates – are relatively free of methodological bias (with the possible exception of egg cannibalism, e.g. Landry 1978). Counts can be straightforwardly converted to production (biomass per unit time), from a knowledge of individual egg mass (e.g. Kiørboe and Sabatini 1994; Uye and Sano 1995).

Egg production has frequently been related to resources, both in terms of concentration (Marshall and Orr 1952; Checkley 1980a; Durbin et al. 1983; Runge 1984, 1985; Beckman and Peterson 1986) and quality (Checkley 1980a; Jónasdóttir et al. 1995), to temperature (Dagg 1978; Uye and Shibuno 1992), and to both factors in combination (Checkley 1980b; Uye and Shibuno 1992). McLaren and Corkett (1981) were among the first to note that egg production may be of similar magnitude to prior somatic growth, and suggested that somatic production of all copepodite stages might be predicted

from a knowledge of egg production rates alone. Recently, measurement of egg production has become one of the most common methods of estimating total copepod production.

However, in addition to being influenced by resources and temperature, both weight-specific egg production (Kiørboe and Sabatini 1995) and somatic growth rates may also be a function of body size (Hopcroft and Roff 1998; Hopcroft et al. 1998b). Given the existence of such body-size and resource-concentration effects on both egg production and somatic growth rates, then the true production of copepods could be severely underestimated if egg production and prior somatic growth rates are in fact unequal. This would be particularly true where resources are commonly limiting to egg production, for example in the broad oligotrophic regions of the ocean.

We asked the simple question: to what extent is egg production related to body size or to food concentration at constant temperature? Here we present laboratory estimates of egg production rates for copepods fed on natural food assemblages from locations around Jamaica, West Indies. We compared these to growth rates estimated for copepodites (Hopcroft et al. 1998b) and nauplii (Hopcroft and Roff 1998) from the same environments. We also assessed the biases in estimates of annual copepod production resulting from the assumption that copepodite somatic growth rates and egg production rates are equivalent. We made such estimates along a trophic continuum from oligotrophic offshore waters (Webber and Roff 1995a,b) through mesotrophic coastal waters (Chisholm and Roff 1990a,b) to eutrophic Kingston Harbour (Hopcroft et al. 1998a).

Materials and methods

Incubations were conducted on female copepods collected from five sites of different trophic status in waters surrounding Jamaica, West Indies (see Fig. 1 Hopcroft and Roff 1998) from 1990 through 1995. The major sampling sites and their characteristics have been described in Hopcroft and Roff (1998). The highest chlorophyll levels occurred at two additional collecting sites deeper inside Kingston Harbour, ~10 mg m^{-3} at the middle harbour and values often in excess of 40 mg m^{-3} inside Hunts Bay (D.W. Webber, unpublished data). Inside Hunts Bay, an embayment of 3 m maximum depth that receives the harbour's only river, temperature and salinity can vary widely (D.W. Webber, unpublished data), and the zooplankton community is taxonomically impoverished (M.K. Webber, unpublished data).

Female copepods were collected using short, slow vertical hauls of 64- and 200-μm mesh WP2 plankton nets of 0.5 m mouth diameter, screened to remove gelatinous predators, diluted and transported to the laboratory for sorting. Concurrent collections for chlorophyll were taken by replicate Niskin bottle casts from the depths of zooplankton collection. One- or two-litre samples were serially size-fractionated through 20 μm Nitex, GF/D (nominal pore size ~2 μm) and GF/F (~0.4 μm) filters under low pressure, and their concentrations of chlorophyll *a* (net-, nano-, and picoplankton, respectively) were determined using fluorometric techniques (see Hopcroft and Roff 1990 for further details).

Dependent on size, individual females were incubated in 70- or 250-ml polystyrene culture flasks ("nanocosms"). For egg-scatterers, flasks were examined after 24 h for the presence of eggs, egg cases and nauplii using a combination of dissecting and inverted microscopes. As we had no means of assessing the reproductively active verses inactive females prior to incubation, incubations where no eggs were produced were discounted. Instances where flasks were contaminated with other copepodites or adults were also discounted. For egg-carriers, flasks were examined frequently (from 1 to 4 h dependent on species and time of day) for the presence/absence of egg-sacs, and the number of eggs per female was documented both during incubation and for freshly caught females. Egg-carriers were followed for up to 7 d (Hopcroft and Roff 1996) to accurately determine the clutch cycle duration.

For all incubations the growth medium was the natural assemblage of phytoplankton, microzooplankton and detritus from the sampling area and depth at which the copepods were taken. Dependent on female size, this growth medium was filtered through either a 64, 100 or 150 μm mesh to remove other nauplii and/or copepodites. The medium was replaced every 24 h for egg-carriers. Incubation flasks were kept at temperatures and photoperiods similar to in situ conditions.

Egg weights, as carbon, were predicted from direct measurements of egg diameters assuming a density of 0.14 ng C μm^{-3} (Kiørboe and Sabatini 1994); predictions by an alternate equation (Uye and Sano 1995) yielded weights consistently lower by ~20%. Carbon was converted to dry weight assuming carbon as 40% of ash-free dry weight (AFDW). For *Euchaeta marina*, egg dry weights were determined by direct weighing. Females' AFDWs were predicted from species-specific prosome length–weight relationships determined for this area (see Hopcroft et al. 1998a), and where appropriate relationships were not available (i.e. *Euterpina acutifrons*, *Oithona simplex*) from direct weights of females. Female instantaneous growth rates (*g*, as egg production) were derived from $g = \ln(W_{\text{Female+Eggs}}/W_{\text{Female}})/t$. This rate has been variably referred to as mass/weight-specific fecundity or growth rate.

For both egg production and growth rate we explored possible relationships between female mass, and resource concentration (as chlorophyll *a*). In addition to simple linear regression on log-transformed data, we also explored the possibility of interaction between both independent variables, and the possibility of more complex relationships (i.e. quadratic) due to evidence of egg production saturating at high resource concentrations (e.g. Checkley 1980a; Runge 1984, 1985; Uye and Shibuno 1992).

Results

Egg production rates were determined for 17 of the most common species from Hunt's Bay, Kingston Harbour, Lime Cay and offshore (Table 1) from a total of over 600 individual egg-producing females. The maximum number of eggs produced per day for an individual was 99 for *Acartia tonsa* in Hunts Bay. In terms of average number of eggs produced, values ranged from as high as 88 eggs d^{-1} for *Acartia lilljeborgi* in Hunts Bay to as low as 3.2 eggs d^{-1} for *Calanopia americanus* at Lime Cay. Within a species, the number of eggs produced daily decreased significantly (*t*-tests, $P < 0.05$) from Hunts Bay to Lime Cay for *Acartia lilljeborgi, Centropages velificatus* and *Temora turbinata* (Table 1). Such differences were not apparent for other individual species, where available data spanned only two of the locations. There was a general trend, across all species, for the highest numbers of eggs produced to be in hypereutrophic Hunts Bay, and for the lowest numbers to be in oligotrophic waters offshore of Discovery Bay.

Egg size tended to increase as female size increased across all species studied (Fig. 1; $r^2 = 0.71$, $P < 0.0001$). Egg production ranged from 0.21 to 10.1 μg AFDW d^{-1}

Table 1 Number of eggs produced daily by female copepods in Jamaican waters [mean ± SE (*n*)]

Taxa	Hunt's Bay	Middle harbour	Outer harbour	Lime Cay	Offshore
Calanoids					
Acartia lilljeborgi	88 (1)	34.5 ± 2.6 (18)	20.2 ± 1.0 (41)	10.4 ± 1.2 (11)	–
Acartia tonsa	69.8 ± 7.4 (9)	–	–	–	–
Calanopia americanus	–	–	4.4 ± 0.3 (7)	3.2 ± 0.5 (10)	–
Centropages velificatus	–	51.3 ± 10.5 (4)	24.6 ± 1.9 (19)	10.9 ± 1.2 (38)	–
Clausocalanus furcatus	–	–	–	–	4.5 (21)
Euchaeta marina	–	–	–	–	3.4 (45)
Parvocalanus crassirostris	–	–	26.9 ± 1.7 (20)	–	–
Paracalanus aculeatus	–	–	–	9.2 ± 0.9 (13)	–
Temora stylifera	–	–	–	24.0 ± 4.4 (7)	23.3 ± 4.8 (12)
Temora turbinata	–	18.3 ± 0.5 (4)	13.9 ± 1.6 (21)	8.0 ± 1.2 (11)	–
Undinula vulgaris	–	–	–	7 (1)	13.5 (5)
Cyclopoids					
Oithona nana	–	–	17.0 ± 4.6 (29)	20.0 ± 3.9 (3.9)	–
Oithona plumifera	–	–	–	–	6.5 ± 1.9 (44)
Oithona simplex	–	–	6.7 ± 1.4 (12)	–	–
Oncaea spp.	–	–	–	–	10.5 (15)
Corycaeus amazonicus	–	–	49.5 ± 12.3 (32)	–	–
Harpacticoids					
Euterpina acutifrons	–	–	21.3 ± 5.3 (40)	17.7 ±7 (19)	–

(Table 2), and increased significantly with female weight (Fig. 2A; $r^2 = 0.38$, $P < 0.0001$, $n = 30$). Egg production was unrelated to chlorophyll in any size-fraction alone (Fig. 2B; $r^2 < 0.05$, $P > 0.05$, $n = 30$). However, in combination with female size, a positive relation to chlorophyll in the >2 μm size-fraction increased the explainable variation ($r^2 = 0.51$, $P = 0.001$ for chlorophyll).

Instantaneous growth rates (i.e. the reproductive growth of females, g_r) ranged from 0.04 to 0.87 d^{-1} (Table 2) and declined from eutrophic Hunts Bay to oligotrophic offshore waters, although differences were not always significant. Growth rates were negatively related to female weight (W_f) (Fig. 3A; $r^2 = 0.29$, $P < 0.0001$, $n = 30$) and positively related to chlorophyll in the >2 μm size-fraction (Fig. 3B; $r^2 = 0.41$, $P < 0.0001$, $n = 30$). In combination these two factors explained 60% of the observed variation in growth rate as predicted by the equation:

$$g_r = 0.081 \ln(\text{chloro} > 2\,\mu\text{m}) - 0.064 \ln(W_f) + 0.0479 ,$$

where chlorophyll is in milligrams per cubic meter and weight is in micrograms. Growth rates of females from different orders appeared to respond similarly to resource concentration and body size, although we lack sufficient data to test this point with statistical rigor. Allowing for a quadratic relationship of growth to chlorophyll in the two factor model, even more variation was explained ($r^2 = 0.72$). Allowing for the interaction of chlorophyll and body size still further improved the explainable variation ($r^2 = 0.82$). This relationship was described as:

$$g_r = 0.23 \ln(\text{chloro} > 2\,\mu\text{m}) + 0.041 \ln(\text{chloro} > 2\,\mu\text{m})^2 - 0.0420 \ln(\text{chloro} > 2\,\mu\text{m} \times W_f) - 0.173 \ln(W_f) + 0.0589.$$

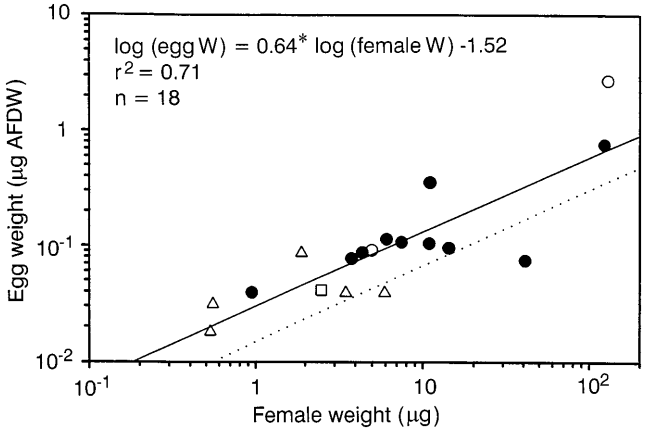

Fig. 1 Relationship between mass of individual eggs and female mass. Broadcast- spawners (*filled*), egg carriers (*open*). Calanoids (●), cyclopoids (△) and harpacticoids (□). Regression from Kiørboe and Sabatini (1995) presented for reference (*dotted line*)

Discussion

Our study is consistent with several others that have demonstrated a positive relationship between egg production and resource concentration (e.g. Marshall and Orr 1952; Checkley 1980a, b; Durbin et al. 1983; Runge 1984, 1985; Beckman and Peterson 1986; Uye and Shibuno 1992). In contrast, the relationship between body size and egg production has received little systematic attention. At the species level, relationships between body size and the numerical rate of egg production have long been recognised, at least within a single species from the same ecosystem (e.g. McLaren 1965; Runge 1984, 1985). It is also well recognised that temperature can influence egg production, both directly in terms of number of eggs produced per day and indirectly by

Table 2 Female weights (μg AFDW), egg diameters (μm), and egg production (μg AFDW d^{-1})/instantaneous growth rates (g) of female copepods from five sites in Jamaican waters

Taxa	Female weight	Egg diam.	Egg production/Instantaneous growth rate				
			Hunt's Bay	Middle harbour	Outer harbour	Lime Cay	Offshore
Calanoids							
Acartia lilljeborgi	7.5	84	9.44/0.82	3.70/0.40	2.17/0.26	1.11/0.14	–
Acartia tonsa	4.4	78	6.10/0.87	–	–	–	–
Calanopia americanus	11	124	–	–	1.55/0.13	1.12/0.10	–
Centropages velificatus	14.2	80–83	–	5.32/0.32	2.35/0.15	1.04/.07	–
Clausocalanus furcatus	5.0	79	–	–	–	–	0.41/0.08
Euchaeta marina	130	293	–	–	–	–	9.20/0.07
Parvocalanus crassirostris	0.95	60	–	–	1.06/0.75	–	–
Paracalanus aculeatus	3.8	75	–	–	–	0.71/0.17	–
Temora stylifera	41	74	–	–	–	1.78/0.04	1.73/0.04
Temora turbinata	6.1/10.9[a]	83–85	–	2.06/0.29	1.56/0.23	0.83/0.07	–
Undinula vulgaris	124	160	–	–	–	5.24/0.04	10.12/0.08
Cyclopoids							
Oithona nana	0.53	46.4	–	–	0.31/0.46	0.37/0.52	–
Oithona plumifera	1.9	77.8	–	–	–	–	0.56/0.26
Oithona simplex	0.55	55.6	–	–	0.21/0.32	–	–
Oncaea spp.	5.9	60	–	–	–	–	0.42/0.07
Corycaeus amazonicus	3.5	59.5	–	–	1.91/0.43	–	–
Harpacticoids							
Euterpina acutifrons	2.5	60–61	–	–	0.87/0.30	0.69/0.24	–

[a] Females inside harbour typically a smaller variety than observed at Lime Cay; lower weight employed for harbour calculations, higher weight for Lime Cay

changing the average size of females at maturity (e.g. McLaren 1965; Vidal 1980a, b; McKinnon 1996).

Between-species comparisons are complicated by size-related changes in both egg weight and the number of eggs produced daily (Kiørboe and Sabatini 1995). Interestingly, while the slope of our relationship between female weight and egg weight is the same as that observed by Kiørboe and Sabatini (1995), the intercept is greater ($P = 0.01$). Given that egg size is less variable than female size within a species (Uye and Sano 1995), then it appears that eggs are relatively larger in tropical copepods than in their cold-water counterparts. Although species-specific differences in life-history strategies can create different combinations of egg size and numerical rates of egg production, even for similar-sized females in the same environment, nevertheless their resultant reproductive growth (g_r) is comparable (see e.g. Hart 1996). Understandably, it may prove difficult to disentangle all these effects prior to examining effects of resource concentration or body size.

It is therefore not surprising that a pattern of decreasing female growth rate with increasing body size has only recently been suggested for copepods (Kiørboe and Sabatini 1995). Our data reinforces such a size-dependent pattern, although we were unable to detect any systematic difference in female growth rates between copepod orders (see Kiørboe and Sabatini 1995) despite the occurrence of such differences in both

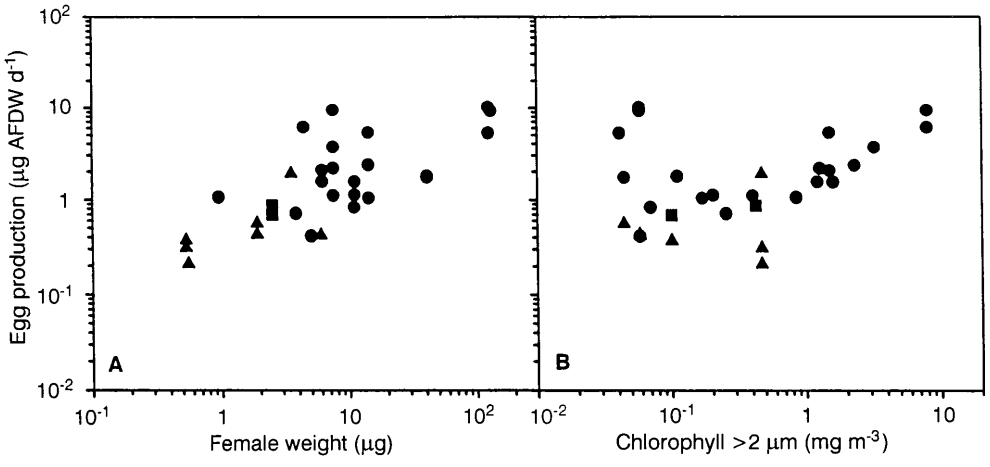

Fig. 2 Scatterplots of **A** female weight and **B** chlorophyll *a* versus egg production rate for calanoids (●), cyclopoids (▲) and harpacticoids (■)

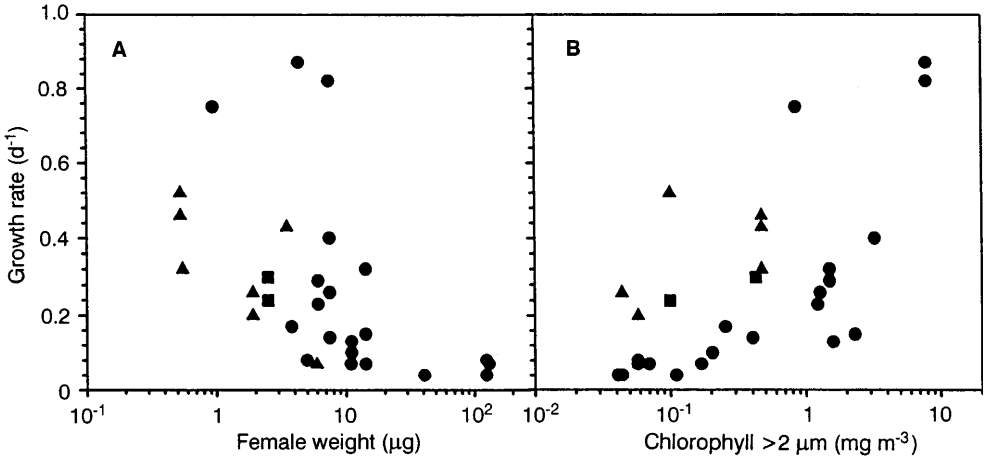

Fig. 3 Scatterplots of **A** female weight and **B** chlorophyll *a* versus instantaneous growth rate (*g*) for calanoids (●), cyclopoids (▲) and harpacticoids (■)

naupliar (Hopcroft and Roff 1998) and copepodite (Hopcroft et al. 1998b) growth rates.

If female growth rate is some composite function of temperature, resources and size, then even within the same species comparisons of egg production (usually as numbers) will not be a straightforward task until all these relationships are more fully understood. Even if we restrict comparisons to closely related species, there may be significant differences in egg production (e.g. *Oithona* species, Tables 1, 2). Furthermore even within a species, there may be pronounced regional (e.g. McLaren 1965) or temporal (e.g. McKinnon 1996) differences in both relative and absolute egg size or mass. Comparison of our egg production and growth rates to other studies suffers from a paucity of data on copepod growth rates at high temperatures and a general lack of data on most species studied (Table 3). Egg production (clutch size and cycle duration) of cyclopoids and harpacticoids has been recently reviewed elsewhere (Hopcroft and Roff 1996) and is not repeated here (with the exception of some more recent data, i.e. McKinnon and Ayukai 1996). Egg production for calanoid copepods from warm waters is generally lower than that observed in our study (Table 3). However, the available data do not yet permit the relative effects of temperature, resources and body size to be separately evaluated. Such a task is further complicated by lack of standardisation on whether egg production is calculated for only egg-producing females, or as the average of all females in a population.

In general, the female growth rates determined here are lower than the growth rates for copepodite stages of these same species at the same locations (Hopcroft et al. 1998b). However, this is not the case for the smallest species. Female growth rates in *Parvocalanus crassirostris*, *Oithona nana*, *Oithona simplex* and *Corycaeus* spp. (all < 3.5 µg for the adult female) were all greater than 0.3 d^{-1}, and comparable to the size-dependent growth rates observed for the copepodites of the same taxa (Fig. 4). In contrast, in species where females are > 3.5 µg in weight, growth rates were lower than those of their copepodites. When growth rates of nauplii, copepodites and female egg production were combined across all taxa, the relationship between body size and growth rate still explained some 45% of the variation in growth rates.

These observations suggest that a synthesis of two apparently divergent views is now possible. The first view is that the production of all copepodite stages can be predicted from a knowledge of egg production rates alone (e.g. McLaren and Corkett 1981; Berggreen et al. 1988; Fryd et al. 1991). The opposing view is that egg production is less than somatic production (e.g. Peterson et al. 1991; McKinnon 1996). These apparently disparate views may have arisen because some studies were conducted under conditions of non-limiting resources, whereas others were conducted under conditions of limiting resources. When resources are not limiting, growth rate may be approximately constant across all developmental stages within a species, including egg production. However, when resources become limiting – in a size-dependent manner – then copepodite stages exhibit higher growth rates than adults, due to the differential availability of appropriate resources under non-optimal conditions (see arguments in Hopcroft et al. 1998b). Such differences in growth rates between copepodites and adults should increase as resources become progressively limiting, and with the absolute size of the adults. Interestingly, although Kiørboe and Sabatini (1995) argue that there is no size-dependent pattern to somatic growth rate, they also argue that female growth rate (their "weight-specific fecundity") declines with female size. Their findings are consistent with our data because, as female size increases, differences between somatic and reproductive growth will become apparent under conditions of limiting food resources.

When growth rates are resource limited in a size-dependent manner, then equating growth rates in all copepodite stages to egg production rates is unfounded. Discrepancies between reproductive and somatic growth rates will increase with the degree of resource limitation and the size of females. To illustrate this discrepancy, we calculated the annual production of copepods in outer Kingston Harbour (Hopcroft et al. 1998a) in three ways:

Table 3 Egg production rates for warm-water copepods. Summary limited to values determined directly on natural food resources at temperatures in excess of 20°C. For summary of non-calanoids see also Hopcroft and Roff (1996). Female weights as AFDW, resource concentration expressed as chlorophyll *a* except where noted

Taxa	Temp. (°C)	Female (μm/μg)	Egg diam.	Production (eggs d^{-1})	Growth rate (d^{-1})	Resource (mg m^{-3})	Source
Calanoids							
Acartia erythrea	26		90	13	0.09	~1.5	Checkley et al. (1992)
Acartia fossae	21–23	900/5.1[b]	85	4.5 (0–20)		0.15–0.35	McKinnon and Ayukai (1996)
Acartia omorii	20			36–39		2.2–24	Ayukai (1988)
Acartia pacifica	22		80	9	0.07	~1.5?	Checkley et al. (1992)
Acartia tonsa	19–28			up to 105	up to 180%		Ambler (1985)
Acartia tonsa	20			65		4.8	Beckman and Peterson (1986)
Acrocalanus gibber	21–29	750–930/–	84	5–40	0.21_{MAX}	0.10–1.54	McKinnon and Thorrold (1993)
Acrocalanus gibber	24–30	745–840 / 3.5–7.0[b]	90–98	–	0.5–0.28	0.23–2.5	McKinnon (1996)
Acrocalanus gracilis	21–29	–	–	8–25	0.21	0.10–1.54	McKinnon and Thorrold (1993)
Bestiola similis (A. inermis)	25–29	–	–	5–17		–	Kimmerer (1984)
Anomolocera ornata	20–22			10–184			Tester and Turner (1990)
Calanopia spp.	~20	–/–	–	4.6 (0.8–8)		~0.1?	Kimmerer et al. (1985)
Centropages furcatus	22–29		81	20–30	0.05	0.9, 0.1	Checkley et al. (1992)
Centropages typicus	20	–/30–60	70	~100		>1.0	Dagg (1978)
Centropages typicus	20–22			98.7			Tester and Turner (1990)
Parvocalanus crassirostris	21–23	390/0.93[b]	66	7.4 (0–21)		0.15–0.35	McKinnon and Ayukai (1996)
Paracalanus sp. *(parvus)*	20–22	640/ –	72	4–21		0.15–1.2	Checkley (1980b)
Paracalanus sp.	18–23	610–775/–	82.5	4–67	0.03–0.4	0.26–15	Uye and Shibuno (1992)
Temora longicornis	21			19.9		~3	Peterson and Kimmerer (1994)
Temora stylifera	20–22	1000/ –	72–78	~20 (69_{MAX})		–	Razouls (1974)
Undinula vulgaris	26–27	2600/181	160	6.4 (0–15.7)	2.1%	35–225 POC	Park and Landry (1993)
Cyclopoids							
Oithona attenuata	21–23	340/0.55[b]	44.5	6.5[a]		0.15–0.35	McKinnon and Ayukai (1996)
Oithona simplex		270/0.31[b]	53	16[a]		0.15–0.35	McKinnon and Ayukai (1996)

[a] Recalculated for egg-carrying females only
[b] Units as carbon

Table 4 Annual copepod production in outer Kingston Harbour (Hopcroft et al. 1998a) and Lime Cay (Hopcroft, unpublished data) calculated in three ways: from direct measures of naupliar-somatic, copepodite-somatic and female-reproductive growth rates (*NCF*); from direct measures of naupliar-somatic and copepodite-somatic rates, and applying copepodite rates to females (*NC*); and using only the egg production rates reported in this paper and applying them to all stages (*F*). All values in kJ m^{-2} yr^{-1}, with percentage contribution (excluding exuvia) in parentheses

Location, method	Naupliar	Copepodite	Female	Exuvial	Total
Harbour					
NCF	174 (11)	936 (59)	475 (30)	93	1679
NC	174 (9.8)	936 (52.7)	665 (37.5)	93	1869
F	123 (10.7)	544 (47.6)	475 (41.6)	56	1198
Lime Cay					
NCF	65 (10.2)	488 (77)	82 (12.9)	46	681
NC	65 (7.4)	488 (55.8)	321.3 (36.8)	46	921
F	24 (10.2)	141 (77)	82 (12.9)	14	261

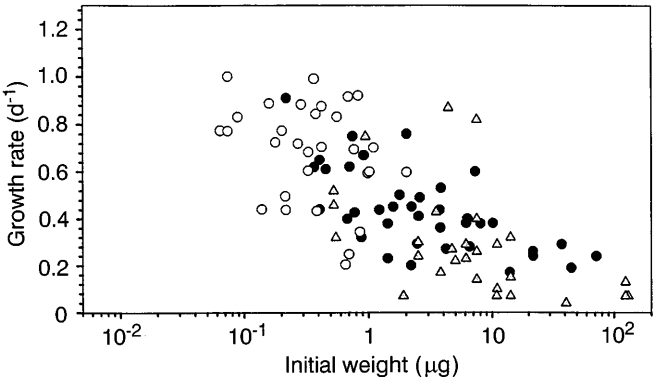

Fig. 4 Scatterplots of weight versus instantaneous growth rate (*g*) for copepods. Somatic rates for calanoids (*circles*) are from Hopcroft et al. (1998b), from nanocosm (*filled*) and microcosm (*open*) incubations. Egg production (*triangles*) for all orders

first, from the direct measures of naupliar-somatic, copepodite-somatic and female-reproductive growth rates themselves; second, using the direct measures of naupliar and copepodite somatic growth, but applying the copepodite growth rates to adult female biomass to estimate female reproductive growth; third, using only the egg production rates reported here applying them to all stages (Table 4). The second method overestimated production as 1869 kJ m^{-2} yr^{-1} (i.e. by 11%); the third method underestimated production as 1198 kJ m^{-2} yr^{-1} (i.e. by 40%). In both methods the relative importance of female egg production was inaccurately overassessed.

The magnitude of the error is increased further in moving from productive coastal to less-productive oceanic waters. At the Lime Cay station (Hopcroft, unpublished), the second method overestimated annual production by 35%, while the third method underestimated it by 260%! Differences will be even more pronounced in oligotrophic offshore waters. Clearly, if egg production rates alone are employed to calculate total copepod production, then the actual production (of somatic growth) must be severely underestimated where larger species predominate and where resources are commonly limiting to egg production, i.e. in the vast oligotrophic regions of the ocean, particularly tropical and subtropical offshore waters. This further emphasises the point that greater attention should be paid to small species and earlier developmental stages in the quest to understand the flow of energy in marine ecosystems. Unfortunately, the severity of food limitation cannot be deduced without comparison of egg production to the traditional and labour-intensive incubation of early copepodite stages – the very task the egg-production technique was designed to avoid. Other non-traditional methods (e.g. Roff et al. 1994) must be explored to facilitate rapid, accurate determination of growth rates for all copepod developmental stages.

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